A Note on the Anatomy of the Circumesophageal Ganglion Complex of Several Doridacean Nudibranchs

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(2 Text figures)

Interest in the electrical properties of large identifiable neurons has led to detailed studies of the nervous systems of many gastropods. In the process of mapping large neurons within the circumesophageal ganglion complex of several doridacean nudibranchs (*Archidoris montereyensis* (Cooper, 1862), *Anisodoris nobilis* (MacFarland, 1905), and *Austrodoris odhneri* (MacFarland, 1966)), I have found a disagreement in the standard literature concerning the locations of the pedal and pleural ganglia. Alder & Hancock (1845: plt. II) (see Figure 1A) and Hancock & Embleton (1852: plt. XVI) (see Figure 1B) show the circumesophageal ganglion complex of *Doris tuberculata* to consist of centrally located dorsal cerebral ganglia, pleural (brachial) ganglia lying more caudal and somewhat ventral, and most laterally and ventral to these, the pedal ganglia. These early works show nerves from the most lateral ganglia (labelled pedal) coursing to the foot while most of those from the ganglia labelled as pleural (brachial) run to the mantle. MacFarland (1966: plt. 36) (see Figure 1D) interchanges the positions of the pedal and pleural ganglia, placing the pleural most lateral and ventral and the pedal most caudal. This report discusses staining and electroanatomical approaches to establishing the identity of these two ganglia.

Specimens of *Archidoris* or *Austrodoris* were obtained inter- or subtidally from the waters around San Juan Island, Washington. Animals were pinned to a wax-bottomed dish under cold sea water. A midline dorsal incision was made in the mantle from between the rhinophores to the circumanal gill plume. The mantle was pinned open and the viscera, except for the esophagus and buccal mass, were removed. This procedure left intact the central nervous system and the major nerves to the mantle and foot. The nerves were stained for easy identification by the application of a solution of methylene blue in sea water to the preparation. The epineural sheath enclosing the ganglion complex was removed after it had been softened by application of pronase.

Camera lucida drawings and photographs of the ganglia and major nerves were made at various magnifications. Single nerves were carefully lifted onto bipolar hook electrodes and stimulated with single 0.1 sec, 40 V pulses, while the animal was observed for gross muscular contractions.

Examination of preparations vitally stained with methylene blue allowed nerves to be traced to fine terminal branches. The large nerve (no. 2, Figure 1C) which runs caudally from the ganglion lying most laterally and ventrally to the others appeared to send numerous branches to the region of the foot. The major caudal trunk (no. 1 or no. 3, Figure 1C) from the most caudal ganglion innervated only the lateral aspects of the animal, presumably the mantle.

Major nerve trunks from the two more laterally lying ganglia were stimulated to determine further their regions of termination. Stimulation of nerves labelled 1 and 3 in Figure 1C caused contraction of the mantle while stimulation of the nerve labelled 2 produced a discrete contraction of muscles of the foot. These observations are consistent with the ganglion naming scheme used by Hancock and co-workers.

A final bit of inferential evidence in favor of the large, most posterior ganglia being pleural instead of pedal comes from observing cells in ganglia with the epineural sheath removed. One might expect from the cell mapping of pleural and pedal ganglia in *Tritonia* (Willows & Hoyle, 1967) that the cell locations in the two pedal ganglia would be very symmetrical while those in the two pleural ganglia would be asymmetrical. Cells are quite asymmetrically located in these two posterior ganglia in *Archidoris* and *Austrodoris* – most strikingly a large white cell can be observed in the left but not in the right ganglion.

The early drawings of the central nervous system of *Doris tuberculata* (Cuvier, 1805), presented by Hancock & Embleton (1852) thus appear accurately to represent that observed in the species of doridacean nudibranchs studied here. That is, the conically shaped cerebral ganglion lies most rostrally sending nerves to the buccal mass, rhinophore, mouth, eye, oral tentacles and the cerebrobuccal connective. Lying most caudally are the oval pleu-

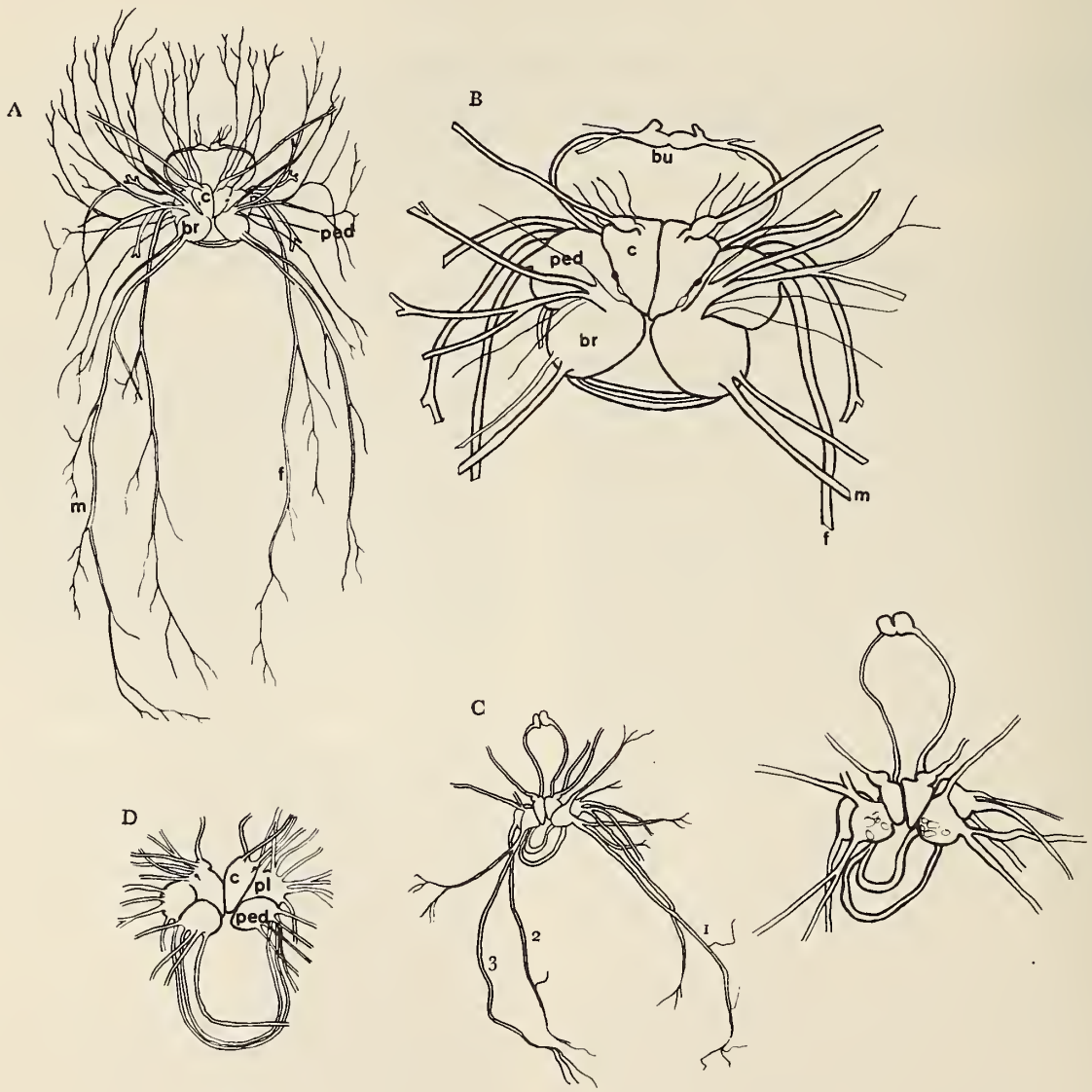
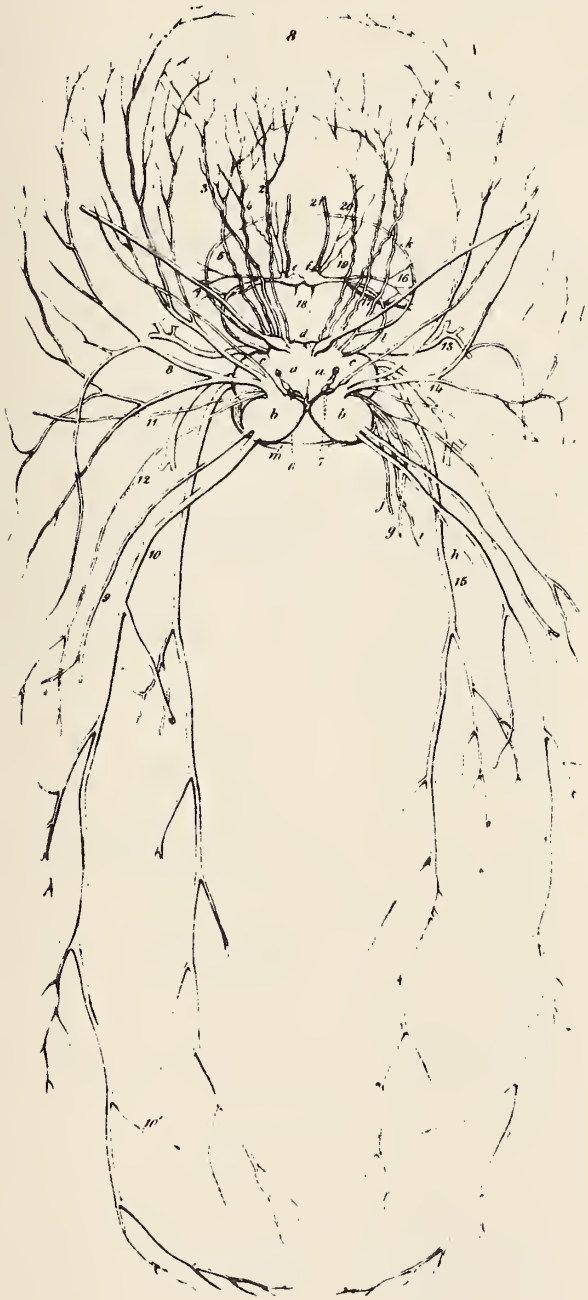


Figure 1

A. Drawing of the central nervous system of *Doris tuberculata*; after plate XVI in Hancock & Embleton (1852). B. Circumesophageal ganglion complex of *Doris tuberculata*; after plate I in Alder & Hancock (1845). C. Camera lucida drawing of a vitally stained preparation of *Austrodoris odhneri*. Drawing on the right is 2½× the magnification of that on the left. Nerves labelled 1, 2, and 3 are discussed in the text. D. Circumesophageal ganglion complex of *Austrodoris odhneri*; after plate 36 in MacFarland (1966). Abbreviations used throughout this figure: c – cerebral ganglion; pl – pleural ganglion; ped – pedal ganglion; br – brachial (pleural) ganglion; bu – buccal ganglion; m – nerve to mantle; f – nerve to foot



ral ganglia from which course nerves principally to the mantle. Finally, lying somewhat ventral to these other two ganglia are the pedal ganglia, the nerves of which innervate the foot. Because of the need for such a drawing by those involved in studies on these animals and because of the inaccessibility of this published figure, it is reproduced here as Figure 2.

ACKNOWLEDGMENTS

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(← adjacent column)

Figure 2

Reproduction of figure 8 of plate XVI in Hancock & Embleton (1852), showing the central nervous system of *Doris tuberculata*. a – cerebral ganglion. b – pleural ganglion. c – pedal ganglion. d – olfactory ganglion. e – buccal ganglion. f – gastroesophageal ganglion. 1 – olfactory nerves. 2 – nerves supplying upper portion of channel of mouth and lip. 3 – nerves to oral tentacles. 4 and 5 – to the sides and lower portions of channel of mouth and lip. 6 – optic nerves, each having at its origin a small ganglion. 7 – statocysts. 8 and 9 – nerves supplying anterior portions of mantle. 10 – nerves to posterior portions of same. 10′ – to ganglia of the stomatogastric system. 11 and 12 – nerves to side of body. 13, 14, and 15 – nerves to foot. 16 and 17 – nerves to buccal mass. 18 – nerves to radula. 19 – nerves to salivary glands. 20 – nerves to top of esophagus. 21 – nerves passing down esophagus and united to two large ganglia of the stomatogastric system. g, h, i, and j – nerves from visceral ganglion. l – cerebro-buccal connective. m – pedal commissure